Seed Research 47(1): 1-14, June, 2019

Influence of Physiological and Environmental Factors on Groundnut Seed Development, Quality and Storage : An Overview

PC NAUTIYAL AND SHIV K YADAV*

Division of Seed Science and Technology, ICAR-Indian Agricultural Research Institute,
Pusa campus, New Delhi - 110012, India
*sky_sst@yahoo.com

(Received : January 2019; Revised : April 2019; Accepted : May 2019)

Abstract: One of the major considerations to attain food security is the use of quality seed which helps in higher production per unit area. Good quality seed is better in terms of genetic purity, physiological maturity and free from seed borne diseases and disorders. Production of better quality seeds starts effective and efficient flowering, pollination and fertilization to seed development is a challenge for increasing food demand. Being an oil seed, groundnut losses its viability soon and seed quality is affected during pre and post harvest periods. Though, the initial seed quality and storage environment are the two major factors to maintain viability and vigour during storage, the invasion of fungal pathogen also play a major role in decreasing the shelf life of a seed. This review article tries to give an insight into groundnut seed development with regards to maintenance of seed quality. Further, points forefront in the seed industry related to seed longevity, seed vigour, seed priming and maintenance breeding for improving crop productivity under various biotic and abiotic stresses have been addressed.

Keywords: Groundnut, Seed development, Storage, Quality, Physiological, Environmental, factors

The genus *Arachis* has evolved in some unusual niches, ranging from semi-arid areas of north-eastern Brazil to Carrado pockets in Amazon forest, to low, deep-soil alluvial plains and humus clay swamp of the Gran Pantanal. This way groundnut (*Arachis hypogaea* L.) cultivation started from South America and later on spread all over the world, mainly tropical countries ranging between 40ºN and 40ºS. At present China (40.1%), India (16.4%), Nigeria (8.2%), USA (5.9%) and Indonesia (4.1%) are the major groundnut growing countries. Crop is predominantly grown in low-input production system in Asia and Africa and yields are between 700 and 1000 kgha^{-1}.Whereas, in high input system in USA, Australia, Argentina, Brazil, China, and South Africa yield levels are quite high, i.e., from 2000 to 4000 kgha^{-1}[1]. In India, groundnut is mainly cultivated in the states of Gujarat, Andhra Pradesh, Tamil Nadu, Karnataka, and Maharashtra. Groundnut kernel is rich source of lipid (36-54%) and protein (21-36%) along with fibre, sugar, starch, vitamin E, niacin, falacin, calcium, phosphorus, magnesium, zinc, iron, riboflavin, thiamine and potassium. The kernels are consumed directly as raw, roasted or boiled, used in the preparation of various confectionary items and oil extracted from these is used for cooking purpose. Haulm issued as animal fodder while oil cakes are feed for animals and poultry birds.

Groundnut is an annual legume and has multiple uses that make it an excellent cash crop for domestic markets as well as for foreign trade in several developing and developed countries. In India aflatoxin contamination is a serious concern in export of groundnut [2]. Seed size is large and its multiplication ratio is quite low (1:5 to 1:10). Seed for sowing require about 100 to 150 kgha^{-1}.Seed development is hypogeal and late seed maturation is characterized by acquisition of functional traits including germination, desiccation tolerance, dormancy and longevity, and influenced by several environmental factors. Seed is stored as pod (in-shell) and shelling is performed only 10-15 days before sowing. This review is focused on environmental influence on groundnut seed development, maturation, curing, drying and storage with regards to maintenance of seed quality and genotypic variations for these parameters. Further, issues associated with seed longevity, seed vigour, seed priming and maintenance breeding for improving crop productivity under various biotic and abiotic stresses have been addressed.

Flowering

Groundnut cultivars belong to varieties, i.e., *fastigiata* (Valencia) *vulgaris* (Spanish) and *hypogaea* (Virginia) [3]. Each of these botanical varieties has different

plant, flowering, pod and seed characteristics [4]. The transition from vegetative to reproductive development is an important phase in any plant which changes its life cycle. Therefore, plants have evolved an intricate genetic network that controls the onset of flowering in response to environmental and endogenous signals such as day length, temperature, hormonal status and carbohydrates, especially trehalose-6-phosphate (T6P) [5]. Groundnut flower is typical papilionaceous, zygomorphic and self-pollinated with about 2% out crossing. Flower morphology and anatomy is widely described by various workers [3, 6]. The flowering pattern varies within and between botanical types, Spanish type flower relatively early and have a broader first flowering peak whereas in Virginia flowering is late and have multiple flowering peaks [7]. Whereas, number of flowers per plant ranges between 40 and 250 in Virginia and 98 and 137 in Spanish types [8]. Flower bud becomes visible 36 to 48hours before anthesis and remains between 6 and 10 mm long just before 24 hours of anthesis whereas during night hour's elongation of hypanthium is faster and the flower reaches the maximum length of 50-70 mm at the time of anthesis. Flower open normally at sunrise, but this process may be delayed by low temperatures and poor radiation. Base temperature for time to first flower is 10.8°C and total cumulative degree days required for flowering are 538, flower production is reported optimum at 25/30°C (day/night temperature) in glasshouse [9]. While, Wynne *et al.* [10] found that greater fruit production of plants grown under short days was not because of differences in flowering intensity, but by the factors that occurred after flowering. Influence of high temperature (40/28°C, day/night cycle) on rate of appearance of flowers is reported to be faster [11]. Flower buds are sensitive to high temperature, especially during 3 to 5 d before anthesis [12]. This is mainly due to exposure of flower buds to high temperature that coincides with microsporogenesis [13, 14] and leads to low pollen viability, poor anther dehiscence, and male sterility. This is attributed to early degeneration of tapetal layer [15, 16] and depletion of carbohydrates in developing pollen [17]. On the other hand, ambient RH is positively associated with daily production of flowers [18]. In addition, influence of higher planting density on flowering rate and blooming period is negative [19]. In addition, closer spacing of plants suppresses the formation of the late flowers [20]. Day-length affects time to first-flower either long days or short days may hasten first-flower appearance [21, 22] whereas Bagnall and King [9] reported that short days promotes flowering as compared to long days. It is also suggested that groundnut is a day-neutral plant [23] while Bell *et al.* [24] reported that photoperiod effects could be seen only at very low quantum. In addition, water deficit stress during vegetative phase followed by two frequent irrigations is helpful in synchronizing flowering in Spanishtype thus leading to higher productivity [25]. It is also reported that plant memories of stress event can be inherited from plant to offspring through a process known as transgenerational stress memory and in groundnut it is suggested that water availability in the plant generation could be responsible for increased seed quality and vigour including root characteristics [26].

Pollination, Fertilization and Peg Formation

After fertilization a mature pod develops in about 60 days [27] whereas lower humidity during pod development is detrimental for embryo development [18]. Pollen remains viable at 90-95% humidity and at high temperature cycle, i.e., 32/22 and 36/26ºC, and viability may decreased near about zero at 44/34ºCcycle [28]. After fertilization, growth of ovule and embryo is light-dependent, for instance, white, red or blue radiation inhibits ovule growth while exposure to darkness or far-red light stimulates it especially during the first 10 days. It is also illustrated that there is photoreceptor that regulates ovule growth, i.e., Phytochrome located in maternal ovular tissue and transmit developmental signal to the embryo [29, 30]. Therefore, after fertilization peg formation take place and exhibits positive geotropism to keep embryo under soil for further growth. In addition, failure of peg penetration into the soil leads formation of aerial pod and auxin and auxin response genes play an important role in this process [31]. Further, groundnut has a unique characteristic that ovaries of pollinated flowers can remain dormant for several weeks and resume active seed development when favourable conditions prevail [32]. In addition, supply of nutrients, such as, sugars, proteins and inorganic other than calcium are transported through gynophores to developing pod. Calcium is poorly transported through the phloem of gynophore [33, 34].

Seed Development

In the development of seed photoperiod and temperature interaction play important role in adaptation of genotypes to new environment, i.e., under the soil [23, 9]. Both high and low temperatures affect crop maturity and duration could be short in humid tropical and sub-tropical

environments [35] whereas photoperiod and temperature interactionwas significant for number of peg and pod development [36]. In addition, total growth period may be shortening from 176 days at 23ºC to 151 days at 18ºC temperatures. Similarly, total crop duration of cv. Robut 33-1 increased from 95 days at 31ºC to 222 days at 19ºC [37]. In addition, exposure to high air and/or high soil temperature significantly reduced total dry mass production, partitioning to pods and ultimate yield [38]. In a study on illustrating high air and soil temperatures indicated that there is no significant effect on total flower production,however, the proportion of flowers setting pegs and hence fruit number was significantly reduced. On the contrary high soil temperature significantly reduced flower production, the proportion of pegs forming pods and 100-seed [39, 40]. In addition, high heritability estimate coupled with high genetic advance were recorded in number of pods plant^{1}, number of seeds plant^{-1}, seed yield plant^{-1} and 100-seed mass [41]. In general, there is report on interactions between the major ABA signalling pathway and other signalling factors in stress response and seed development [42].

Seed Harvest and Maturity

Groundnut is an indeterminate crop the seed lot is having seeds of various maturity stages which adversely affect its chemical composition, germination, vigour and various seed characteristics [41, 43]. There are reports that plant stand and associated yield variations exists mainly due to the variation in seed maturity classes within seed lots [44, 45]. Also, it is emphasised that stage of maturity at harvest is the primary factor in the seed production chain that influences seed vigour [46]. An elaborative account on major events and regulatory pathways related with seed longevity and key processes of desiccation tolerance have been widely reviewed in orthodox seeds [47]. Groundnut at harvest possesses pods with broad range of maturitywhereas processing unit requiresmature seed with uniform size and quality. Researchers have been working with the objectives to obtain a high yielding variety with higher percentage of sound mature kernels. Several seed maturity aspects such as biochemical, physical, internal pericarp colour, tannin and sugar contents, seed hull maturity and hull scrap have been taken into consideration to develop suitable method for seed maturity prediction [48, 49]. Based on testa texture and colour and kernel shape, a visual method was developed to determine maturity of shelled peanut [50]. A biochemical method based on the fact that arginine decreases drastically as groundnut seed mature and this was used in measuring seed maturity index [51]. A practical method for the use of farmers and breeders however is when more than 75-80% pods in case of Spanish/Valencia and 70-75% pods in case of Virginia cultivars show internal pericarp darkening the crop is considered ready to harvest [52]. For commercial use, it is suggested that 100-seed mass could be taken as index of average seed mass and seed with an average mass of 0.55 g or more could be preferred [53]. There is report that supplemental Ca will be the most likely nutritional problem of groundnut production seed quality in acid, sandy and low cation exchange capacity soils [54].

Further, influence of seed maturity on germinability and vigour was reported in various Spanish and Virginia cultivars [45, 55]. Also, Spanish and *Virginia* market types exhibited higher germination with small and medium seeds as compared to large seeds while field emergence was higher in large seeds of Spanish and medium seeds of *Virginia* [44]. Utilization of reserve food material analysed in cultivars belonging to three different seed-weight groups showed that both medium and higher seed-weight are efficient in utilization of reserve food material than lower seed-weight. Further, it was concluded that for adequate food supply from cotyledons during seed germination, 100-seed mass should be >30g [56]. In Spanish groundnut higher number of mature pods, germination and vigour were obtained when harvest was performed between 94 and 101 days after emergence [57]. Among five *Virginia* and Spanish varieties, overall, germinability and seedling vigour was reported to be higher in optimum mature than natural and immature seeds. In addition, in large number of germplasm days to maturity have been reported higher in *Virginia* (143) followed by *fastigiata* (128) and *vulgaris* (122) while 100-seed mass and kernel yield were higher in *Virginia* [58]. In groundnut, a common problem of pre-harvest invasion of *Aspergillus* fungus exist under water deficit stress and high temperature conditions during seed maturity. This may reduce germinability [59] and increase aflatoxin production due to rapid synthesis of carbohydrates in seed [60]. In addition, seed of wild species is quite similar to the cultivated groundnut, except that they are much smaller in size.

Seed Curing and Drying

It is reported that genetic variation and environmental conditions during seed maturation, within seasons

and across seasons play important role in storage of groundnut seed [61]. Usually, groundnut pods are harvested at *mc* (moisture content) between 35-60% and need to be dried along with the vine for 2-3 days. After drying, pods *mc* while being with vine need to be brought down to 18-20%. At this *mc* pods could be detached from vine by mechanical threshing whereas for hand thrashing 15% *mc* is desirable. Thus drying of seed along with vine is an important aspect in groundnut seedproduction for making glassy state prefect [62]. There are various conventional and non-conventional methods for pod drying are mentioned in the literature, such as, windrow, small or large random heaps and shade drying. Also, different methods for pod drying have been developed, for example, Directorate of Oilseeds Research Method (DOR-method) [63] the National Research Centre for Groundnut method (NRCG-method), tripod shade drying method [64]. Pods dried directly under sunrays such as wind row may lose germinability as pod temperature may exceed beyond 40°C especially during summer season, this could be detrimental to seed tegument layer [65, 66]. In addition, application of lime in the field increases the tegument thickness and decrease the central cavity mainly in the exo-testa cells [67]. Also, role of late embryogenesis abundant proteins (LEAs) as protectors helps seed to tolerate desiccation at maturity [68, 69]. In general, in orthodox seeds, determinations of function of ABA-regulated gene products and genes that contain information of desiccation tolerance and role of LEA proteins in desiccation tolerance together with sucrose have been extensible reviewed [70, 71]. Further, if initial *mc* of pods is not reduced properly, it may influence lipid metabolism and seed quality adversely at higher pod moisture [72]. After harvest substantial percentage of the pods are left in the soil, such left over pods should not be mixed with the main seed lot because the chances of contamination are more in the soil [73]. Percentage of left over pods depends on peg strength and it is poor in *Virginia* than Spanish types [74]. Finally, pods could be tested for thorough drying by following method: i) pods should give retelling sound when shaken, ii) if seed is pressed it should easily split into two cotyledons, and iii) on rubbing hard on the surface, a portion of the seed coat peels off mainly in *vulgaris* type [2]. The relationship between the glassy state in seed and storage stability has been established by Sun [75].

Seed Storage

There are need to store seed for various purposes, such as, germplasm conservation, maintenance breeding, warehouses of seed co-operation's and farmers storage conditions.

(i). Germplasm conservation and maintenance breeding

Seed is critical and vital unit for germplasm preservation and its utilization for enhancing productivity. Groundnut seed is having wide variation in their size, shape and colour, testa or seed coat is thin and papery. It is common observation that seed coat colour during storage turns to brownish or dark tan from pinkish mainly because of Millard reaction a non-biochemical activity. In general, it is reported that vitamin E is essential for seed longevity and preventing lipid peroxidation during germination [76]. Seed coat consists three unicellular layers, i.e., the epidermis or sclerenchyma, middle parenchyma and inner parenchyma. These layers represent the integuments of the maturing ovule and are maternal in origin. The surface as well as the transverse sections of testa shows wide diversity. Therefore, groundnut cultivars may be classified based on the size of wax layer, the joining of the epidermal cells, thickness of cell walls and presence of cracks in epidermal layer. Ideal conditions for groundnut seed storage are 10°C and 65% RH resulting seed *mc* around 6% [61]. When seed is stored in warehouses without climate control, maintaining these conditions become difficult. It is also reported that seed (in-shell) stored at 15°C and 79–83% RH germination remains above 80% for more than 150 days whereas the same seed lot when stored at 15°C and 85–89% RH, germination decreased dramatically to 30% in 80 days [77]. Gene banks deals with germplasm conservation for long term at –20°C with seeds having 85% germination and seed *mc* between 3 and 7%. Active/ working collection is stored for medium term at 4°C and 20-30% RH with seeds having *mc* between 7 and 8% and germination >80%. The medium-term storage retains >65% seed viability for 10-20 years. Seeds stored at 10°C and 45% RH had good germination even after 20 years [52]. Groundnut seed, however, could be stored at low *mc* (3.3%) for 11 years at ambient temperature [78]. Also, for maintaining valuable genetic resource in breeding programme seeds are stored with $CaCl_2$ or silica gel in sealed desiccators [79]. Use of desiccant helps

to keep seed *mc* below <10% to avoid water activity. In addition, studies conducted at ICRISAT have concluded that polyethylene bag (600 or above gauge thickness) is the best material for maintaining seed storability for utilization of genetic material in breeding programmes or at the farmers storage conditions. In addition, detailed study was conducted by ICRISAT to assess the relative storability of eight cultivars and reported that storage of groundnut seed is regulated by several intrinsic such as genotypic variability, seed morphology, initial seed *mc* and dormancy, and extrinsic such as storage temperature, RH and storage container/packaging material, factors.

(ii). Storage at farm level

Seed in-shell remains well protected from outside environment along with inside CO_2 that prevents it from rapid deterioration and mechanical damage) [56, 65, 80]. In addition, rapid loss of viability is a major problem of rabi/summer season seed lots [66, 81] however there are varietal and seasonal variations in longevity and genotype with high viability potential have been identified [82]. For example, in Indian groundnut is harvested during different months based on cropping season and seed lots require 4-8 months storage for the sowings in ensuing season. For example, rainy season seed lot is harvested in October and stored for 4 months for sowing in summer, and 8 months for next rainy, seasons. Conventionally groundnut is stored in-shell in gunny bags at relatively dry and ventilated place. In some areas groundnut is cultivated only in summer or *rabi* seasons and seed lots could not be stored for the next season sowing due to rapid loss of germinability. Since, seed lots collected in this season are stored for a long period that too initial phase of it passes through high RH and temperature during rainy season (June-September) this makes the seed to exceed the limit of safe *mc*, i.e., >10% [79]. Farmer's seed lots from summer season collected in June from Bhuj in Gujarat, lost germinability rapidly when stored in gunny bags at ambient laboratory conditions at Junagadh within 4 months [83]. A technology has been developed for storage of seed(in-shell), i.e., after through drying, seed initial *mc* between 7-8% could be stored in polyethylene lined gunny bags with desiccant like silica gel or calcium chloride ($CaCl_2$, anhydrous) @250 g for 30 kg seed [59, 84, 85]. This technology was demonstrated successfully in coastal (Bhubaneswar) and inland (Bargadh) areas of Orissa [66] the hot spots for the loss of seed viability in summer groundnut. On the other hand, seed lots collected during *kharif* season may be stored in well ventilated place in gunny bags for the next sowing with initial *mc* between 6-8%, this maintains >80% germinability even after 8-10 months of storage [86].

(iii). Seed quality deterioration during storage

A model for seed quality deterioration in groundnut is proposed based on the work done by Walters, Wilson and McDonald, McDonald and Morton [87-90]. Such as, seed *mc* between 6 and 14% prevent lipid peroxidation activity and keep it to minimal because sufficient water is available to serve as a buffer against autoxidation, but is insufficient to activate lipoxygenase-mediated free radical production. Whereas, below 6% *mc*, lipid autoxidation may be the prime factor in seed deterioration as water is unavailable to buffer the free radicals. In addition, above 14% *mc*, the increasing water content enhances the activity of oxidative enzymes, such as lipoxygenase and production of free radicals. As seed *mc* increases, autoxidation increases and is further accelerated if temperature increases. Elevated temperature and RH during storage allow embryonic axis to absorb moisture from outside environment. This increased *mc* and temperature may cause the glass state of water to reach T*g* this changes water into amorphous state. The reactive oxygen species are generated and they attack the unsaturated lipids of cellular membranes, especially mitochondria leading to produce a chain reaction of autoxidation. Thus, cellular membranes become porous and during imbibition there is increase in leakage of solutes. Thus greater the damage during storage, longer the repair phase during imbibition, if damage is too severe, the seed becomes non-viable. Hence, initial phase of seed imbibition becomes crucial in repair of cell membrane, proteins and DNA components.

In addition, several other factors influence the vigour and viability, such as, genotype, maturation growth conditions, physiological maturity at harvest, initial *mc* mechanical and insect damage and pathogen attack [91]. During seed development, maturation, drying and storage desiccation damage is also related to oxidative processes, as indicated by high levels of ROS-scavenging enzymes and tocopherols [92]. It is also demonstrated that during germination uncontrolled ROS production can lead to oxidative stress and cellular damage, resulting in seed deterioration and impeding germination and early seedling development [76]. Also, cell wall storage polysaccharide during seed maturation is used as a

product of hydrolysis for growth and control of source-sink relationship in developing seedling. This has implication in biotechnological applications for enhancing seed quality [93]. In groundnut, storage time is negatively associated with seed quality parameters and a negative relationship between oleic acid and linoleic acid during seed storage was reported. In addition, both the á-tocopherol and ä-tocopherol values of each grade seed size decreased with extended storage period [94]. Seed accelerated aging experiment also demonstrated that this is mainly because of aging-induced lipid peroxidation by damaging seed membrane tissues. In addition, in two groundnut cultivars, it was reported that accelerated aging inhibited activity of superoxide dismutase, peroxidase, ascorbate peroxidase, and lipoxygenase, despite having difference in seed mass [95]. In addition, reactive oxygen species (ROS) are continuously produced during seed development and have been attributed as only damaging compounds. In an experiment, after imbibition non-dormant seed produced more ROS than dormant seed, and were attributed to the role of ROS in control of seed germination and dormancy release [96].

(iv). Effect of Aspergillus on groundnut seed germination

Seed stored in the stacks in warehouse or farmer's conditions had more incidences of fungi than seed at harvest or seed stored in controlled conditions. In groundnut most of the storage flora is species of *Aspergillus* and *Penicillium*, and are active at RH ranging from 70-90%. In bulk storage problem of unequal distribution of *mc* occurs where no forced aeration system is available and seed become susceptible to storage fungi, and invasion can occur at seed *mc* as low as 13.2% and is based on seed water activity. Species of *Aspergillus* are specific to seed water activity small change in the water concentration may result in colonization by different species [97]. In addition, water activity differs for species and assuming that lipid is non-miscible, thus in groundnut critical *mc* may be computed on the non-lipid portion of seed [90, 98].

Germination and Seed Vigour Tests

The transition from quiescent dry seed to an actively growing photoautotrophic seedling is a complex and crucial trait for plant propagation. In this regard, gene expression in developmental stages of seedling establishment in *Arabidopsis* has been studied in detail [99]. As germination tests are essential to judge the potential of seed to the percentage of normal seedlings and used in seed certification [100]. The standard procedure to assess the extent of deterioration of seed during storage is laboratory germination test using "between the paper method" by following standard seed testing rules as described by ISTA [101]. Whereas, for the interest farmers, it is appearance of seedling on the soil surface, which depends on seed vigour and comprises of properties such as potential for rapid, uniform emergence and development of normal seedlings under a wide range of environmental conditions. Ketring [61] developed a vigour index for groundnut that takes into account seed germination and rate of seedling growth, and was directly correlated with rapidly growing seedlings.In addition, for the assessment of field emergence under water deficit, number of secondary roots was taken into consideration for calculating the SVI [56]. Seed leachate studies have been conducted to assess the role of testand seed vigour and viability of aged seeds [59, 102-105]. A significant negative association between conductivity of seed leachate and germination percentage in groundnut has been reported [65] also in various crops [106]. In addition, ethylene production during seed germination rises prior to any visible sign of growth and peaks twice at emergence of the hypocotyls-radicle when the radicle emerges from the hypocotyl, thus playing important role in seedling vigour [82, 107]. Hence, exposure of seed to high RH during storage may deteriorate quality due to reduced ethylene production. In addition, tetrazolium test is the standard method for evaluating viability potential of seed lots in groundnut [108] and also used to differentiate between dormant and dead seeds in germination test.

The optimum mean soil temperature for seed germination and root growth is between 29 and 30ºC and 30ºC, respectively [109]. At low soil temperatures, i.e., 19 and 22ºC field emergence is reported about 50% [23]. Seed water imbibition is triphasic and germination is epigeal, and carbohydrate is the first energy source utilized by the germinating seed followed by protein and lipids [110]. After emergence cotyledons become green and can supply the food material to the developing seedling at least for 15 days till it becomes fully autotrophic [56]. The hypocotyl is white and is easily distinguished during the early stages of growth, but becomes indistinguishable from the root as the plant matures [7]. Thermal duration from sowing to emergence is reported to vary among varieties during different cropping seasons [111]. It is also reported that

the germination of two seed lots varying in seed vigour may be same at the optimum temperatures, however, under stressed conditions low vigour seed lot may show week seedlings [112]. Ketring[113] reported that 500 mm of water is necessary to produce seeds of high quality, because water deficit stress during seed development affects subsequent seedling vigour [85].

Relationship between Seed Germination and Dormancy

Dormancy is a complex evolutionary trait that temporally prevents seed germination, thus allowing seedling growth in a favourable season. In groundnut, whether seed dormancy is directly associated with longevity or not is not clear but the basic purpose of seed dormancy is to check the viviparous nature of seed to germinate under favourable conditions while being with mother plant. This way seed dormancy may be considered a desirable agronomical trait which is common in Virginia while Valencia and Spanish, types require some degree of fresh seed dormancy [114]. In addition, different parts of seed, i.e., seed coat, cotyledons and embryo have been reported to impart a role in dormancy [115] and short period of dormancy was found more under control of testa than cotyledons. The complexity arises in studying inheritance of seed dormancy when both maternal (testa) and zygotic (cotyledons) tissues are involved in its control [116] while genetic control of seed dormancy has been reported to be monogenic with dormancy dominating over non-dormancy [117, 118]. Also, quantitative inheritance with additive, dominance, and digenic epistatic effects in seed dormancy was reported [119, 120]. High-throughput analyses of transcriptomes have led to significant progress in understanding the molecular regulation.

Such as, gene ontology clustering showed that the functions of polysome-associated transcripts differ between dormant and non-dormant seeds [121]. Thus dormant seed possess different physiological traits during development and maturity than the non-dormant. During storage, seed slowly or some time rapidly breaks the dormancy and it is presumed that there is loss or inactivation of inhibitors present or synthesis of growth promoters increases as dormancy decreases. Groundnut plants having long crop duration such as Virginia possess prolonged seed dormancy than those having shorter crop duration, i.e., Spanish and Valencia [122] however variability in fresh seed dormancy exists among genotypes of short crop duration [114]. Among cultivars prolonged dormancy is reported to be 70 days in M 37, Kadiri 71-1, and Kadiri 2 [123]. In addition, storage temperature may influence the period of dormancy [124].

Seed Hardening and Priming

The term seed hardening was coined in the 20 century to successive cycles of steeping with water and drying for physiological seed enhancement treatment. Later on precise methods for seed invigoration were investigated by involving the imbibition and desiccation processes generally known as priming or invigoration. In groundnut, literature on seed hardening or priming is very scanty, however, some information is available on soaking of seed with hot water to enhanced field emergence under sub-optimal temperature, pre-sowing seed hardening for drought tolerance for summer groundnut sowing [125, 126] and osmoconditioning with PEG for increasing vigour and cold hardness [127, 128]. Joshi *et al.* [129] studied groundnut seed germination under sub-optimal temperature and recorded enhanced germination percentage by osmoconditioning with PEG 6000, while Nautiyal *et al.* [130] tested groundnut seed germination under salinity stress in laboratory. Also, groundnut seeds were primed with $CaCl_2$ and this resulted into improved seed vigour growth and pod yield [131]. It is also reported that seed treated with organic and inorganic nano-particles for enhancing seed quality [132]. In addition, seed priming or pelleting with Ca can improve groundnut establishment under low pH stress in soil [90].

Genetic Improvement

In the perspective of view climate change scenario, it is necessary to develop climate resilient varieties with enhanced and stable genetic improvements. For identifying the traits associated with biotic and abiotic stresses tolerance including pre-harvest aflatoxin contamination are on the top agenda of various groundnut improvement programmes[133,134]. Highly informative genetic and genome SSR markers were identified to facilitate molecular breeding in groundnut [135]. Further, quantitative trait loci were identified for pod and kernel related traits, geocarpy, oil biosynthesis and allergens and a transcriptome map was developed for *A. hypogaea*[136,137]. Janila *et al.* [138] studied molecular breeding for introgression of fatty acid mutant alleles

that enhanced oil quality in high and low oil containing genotypes. Sarvamangala *et al.* [139] identified quantitative loci for protein content, oil content and oil quality while Shasidhar *et al.* [140] studied molecular mapping of oil content. In addition, seed dormancy requires both selective mRNA oxidation and protein carboxylation [141]. Also, germination is controlled by endogenous factors, i.e., abscisic acid (ABA) and gibberellins (GA) these play a major role in regulating early seed germination through the process of dormancy [142]. In this regard two major quantitative trait loci for fresh seed dormancy were identified [143] and genome-wide association of major agronomic traits related to domestication was studied [144]. There are reports that transgenic seeds exhibited over accumulation of heat stress transcription factor and sHSP, this improved germination and vigour under stressed conditions [145, 146]. In groundnut the transcript significantly over-expressed in pod include genes responsible for seed storage proteins and desiccation (LEA) oil production, and cellular defence [147]. Moreover, expression of stress response and protein display in the form of HSPs is indispensable for health and longevity in all organisms [148]. Also, it is reported that essential mechanism for seed vigour testing could be translational capacity, mobilization of seed storage reserves and detoxification efficiency [149]. Work is being carried out in several laboratories to validate the role of the characterised proteins in seed vigour by reverse genetics. For example, using tissue-specific promoters in the genetic transformation, groundnut seed promoter (GSP) region of the gene 8A4R19G1 is being used in genetic engineering in legumes aimed at targeting novel transgenes to the seeds, especially those involved in micronutrient enhancement, fungal resistance and molecular farming) [150]. In addition, DNA binding with one finger (DOF) transcription factors plays important roles in storage material accumulation and morphogenesis of developing seeds in groundnut, and GW 391729 was found related to seed number in fruit, and also possibly related to leaf spot resistance [151]. Insights into the large number of Indian groundnut genotypes covering various aspects related O/L flux regulation and ahFAD2 gene polymorphism have been reported [152]. Many workers have contributed significantly on various aspects, some of important research reported on groundnut seed, since 1950 are listed in table 1.

Table 1. Some important research reported on groundnut seed, since 1950 to 2019.

Research topic	Reference
Report on aerial flowering and subterranean fruit habit in groundnut.	Smith [153]
In groundnut embryo may become dormant for several weeks and it may revive after having favourable conditions.	Smith [32]
Report on photo control of groundnut seed embryo and ovule development.	Thompson et al. [29]
Localization of phytochrome during groundnut embryo and ovule development.	Thompson et al. [30]
Report on DNA binding with one finger (DOF) transcription factors play important role in storage material accumulation and morphogenesis of developing groundnut seed.	Yan et al. [151]
Comparative transcriptome analysis of aerial subterranean pods development provides insights into seed abortion in groundnut.	Zhu et al. [31]
Genomic and transcriptomic analysis identified gene clusters and candidate genes for oil content in groundnut.	Wang et al. [154]
Transgenerational stress memory of seed and seedling vigour of groundnut varies by genotype.	Rowland et al. [26]

Future issues

Following thrust areas were identified for the improvement of seed quality and vigour in groundnut.

1. Since groundnut seed development is under the soil, its preparation for germination phase during seed maturation on mother plant need to be identified, such as, characterization of transcripts both stored and *de-novo* synthesized and stored proteins may help to provide a better understanding. Further, genome-wide gene expression analysis may provide deeper insight into the early phase of seed germination, i.e., imbibition and the subsequent plateau phase of water uptake in which metabolism is reactivated and translation of stored mRNA begins. This phase is also important in understanding the process of seed priming.

2. In addition, there is sulphur amino acid metabolism pathway representing a key biochemical determinant and alteration in hormone levels of the commitment of seed to initiate its development towards germination, especially proteostasis and DNA integrity play a major role in germination phenotype.

3. Seed vigour studies need to be accelerated based on automation and non-invasive methods, i.e., NIR, MIR and X-ray CT to identify traits such as early vigour and tolerance to biotic and abiotic stresses during seed germination and seedling development.

4. Flowering is an important issue in enhancing groundnut productivity, timing of induction of flowering determines to a large extent, the reproductive success of any crop. Especially carbohydrates, trehalose-6-phosphate (T6P) play a crucial role in regulation of flowering by initiating florigen activity. This may be studied to boost synchronised flowering and enhancing seed multiplication ratio as well as productivity. In this regard, there is need to manipulate two flowering peaks that is intrinsic quality of groundnut to a single peak. In addition, optimum RH and temperature are two major factors for groundnut flowering and effective peg formation need to be addressed with respect to climate change phenomena.

5. Relationship between seed dormancy and seed viability during storage is still obscure and need further investigation. In addition, information on seed deterioration during storage is scanty and studies so far have been conducted with limited number of genotypes, therefore, taking large number of genotypes belonging to different market types, need to be focused in view of different agro-climatic conditions. Active oxygen species (AOS) and antioxidants play an important role in seed physiology, therefore, must be used to elucidate the inter play of AOS with hormones by analysing gene expression in contrasting situation using the microarrays, cDNA amplification fragment length polymorphism and proteomic tools.

6. A suitable low cost effective storage strategy for storing groundnut seed (off-shell) in the warehouse to reduce bulk storage of pods (in-shell) needs to be developed. So far, work on seed priming or hardening for germination under sub-optimal temperatures and soil moisture conditions has not been addressed adequately. This may open new areas for cultivation of groundnut in rice fellow.

REFERENCES

1. SINGH AK AND SN NIGAM (2016). Arachis gene pools and genetic improvement in groundnut, In: Gene pool diversity and crop improvement, sustainable development and biodiversity, Rajgopal VR *et al.* (eds), Springer International Publishing, Switzerland. Retrieved from doi: 0.1007/978-3-3-319-27096-8-2.

2. NAUTIYAL PC (2002). Groundnut: Post-harvest, Food and Agricultural Origination of the United Nations, 6, Chaps, Retrieved from www.http: FAO.org/agri/postharvest/compendium/groundnut, pp:1-123.

3. GREGORY WC, MP GREGORY, A KRAPOVICKAS, BW SMITH, AND JA YARBROUGH (1973). Structures and genetic resources of peanuts, In: Wilson CT (ed) Peanuts—Culture and uses. *American Peanut Research Education Association, Stillwater, OK*, **3**:47– 134.

4. KRAPOVIKAS A AND WC GREGORY (1994). Taxonomia del genero*Arachis* (Leguminosae). Bonplandia8:1-187. (In Spanish). (English translation by Williams DE, Simpson CE 2007). *Taxonomy of the genus Arachis (Leguminosae). Bonplandia*, **16** (Suppl.):1–205.

5. WAHL V, J PONNU, A SCHLERETH, S ARRIVAULT, T LANGENECKER AND A FRANKE (2013). Regulation of flowering by trehalose-6-phosphate signalling in *Arabidopsis thaliana Science*, **339**: 704-707.

6. NIGAM SN, MJ VASUDEVA RAO, AND RW GIBBONS (1990). Artificial Hybridization in Groundnut. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Patancheru, AP, India Information Bulletin no. 29**.**

7. VARA PRASAD PV, VIJAYA GOPAL KAKANI AND HD UPADHYAYA (2009). Growth and production of groundnut, in Soils, Plant Growth and Crop Production, (Ed. Willy H. Verheye), in Encyclopaedia of Life Support Systems (EOLSS), Developed under the Auspices of the UNESCO, Eolss Publishers, Oxford ,UK.

8. SASTRY KSK, VR SASHIDHARAN, AA MEKHRI AND G PARAMESWARA (1980). Drought tolerance studies in groundnut, castor and sunflower Final report of ICAR scheme 1974-79, Bangalore: University of Agriculture Science.

9. BAGNALL DJ AND RW KING (1991). Response of peanut (*A. hypogaea* L.) to temperature, photoperiod and irradiance2. Effect on peg and pod development. *Field Crops Research*, **26**: 279-293.

10. WYNNE JC, DA EMERY AND RJ DOWNS (1973). Photoperiodic responses of peanuts. *Crop Science*, **13**:511-514.

11. CRAUFORD PQ, TR WHEELER, RH ELLIS, RJ SUMMERFIELD AND PVV PRASAD (2000). Escape and tolerance to high temperature at flowering in groundnut (*A. hypogaea* L.). *Journal of Agriculture Science*, **35**: 371-378.

12. TALWAR HS, H TAKEDA, S YASHIMA AND T SENBOKU (1999). Growth and photosynthetic responses of groundnut genotypes to high temperature. *Crop Science*, **39**: 460-466.

13. MARTIN JP, S CAS AND H RABECHAULT (1974). Cultures in vitro determine sarachide (*A. hypogaea* L.). Stades du development des boutons floraux microsporogenesis. *Oleagineux*, **29**: 145-149.

14. Xi X-Y (1991). Development and structure of pollen and embryo sac in peanut (*A. hypogaea L.*). *Botanical Gazette*, **152**:164-172.

15. VARA PRASAD PV, PQ CRAUFURD AND RJ SUMMERFIELD (1999). Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. *Annals of Botany*, **84**:381-386.

16. SUZUKI K, H TAKEDA, T TSUKAGUCHI, AND Y EGAWA (2001). Ultrastructural study of degeneration of tapetum in

anther of snap bean (*Phaseolus vulgaris* L.) under heat-stress. *Sex Plant Reproduction*, **13**:293–299.

17. PRESSMAN E, MM PEET AND M PHARR (2002). The effect of heat stress on tomato pollen characteristic is associated with changes in carbohydrate concentration in the developing anthers. *Annals of Botany*, **90**:631–636.
18. LEE TA, DL KETRING (JR.) AND RD POWELL (1972). Flowering and growth response of peanut plants (*A. hypogaea* L.) at two levels of relative humidity. *Plant Physiology*, **49**:190-193.
19. CATTEN P AND A FLEURY (1998). Flower production and growth in groundnut plants. *European Journal of Agronomy*, **8**: 13-27.
20. ONO Y AND K OZAKI (1971).Effect of shading treatments at early growth stage on growth and yield of peanut plants. *Crop Science Japan Proceedings*, **40**: 480-485.
21. SENGUPTA UK, GS SIRONI, TC POKHRIYAL AND MS KAIM (1977). Photoperiodic control of flowering in groundnut (*A. hypogaea* L.). *Current Science*, **46**:271-272.
22. SENGUPTA UK AND A SHARMA (1984). Studies on assimilate transport in relation to yield in groundnut. *Indian Journal of Plant Physiology*, **27**: 232-238.
23. LEONG SK AND CK ONG (1983). The influence of temperature and soil water deficit on the development and morphology of groundnut (*A. hypogaea* L.). *Journalof Experimental Botany*, **34**:1551-1561.
24. BELL MJ, RC ROY, M TOLLENAAR AND TE MICHALES (1994). Importance of variance in chilling tolerance for peanut genotypic adaptation to cool, short season environments. *Crop Science*, **34**:1030-1039.
25. NAUTIYAL PC, V RAVINDRA, PV ZALA AND YC JOSHI (1999a). Enhancement of yield in round nut following the imposition of transient soil-moisture-deficit stress during the vegetative phase. *Experimental Agriculture*, **35**:371-385.
26. ROWLAND DIANE, BARRY TILLMAN, JOHN ERICKSON, PATRICIOMUZOZ AND WILFRED VERMERRIS (2019). Transgenerational stress memory of seed and seedling vigour of peanut (*A. hypogaea* L.) varies by genotype. *Environmental and Experimental Botany*, **162**:541-549.
27. SESHADRI CR (1962). Groundnut. Hyderabad, Andhra Pradesh, India, Indian Central Oilseeds Committee, pp: 274.
28. VARA PRASAD PV, KJ BOOTE, LH ALLEN (JR.) AND JMG THOMAS (2003). Super-optimal temperatures are detrimental to peanut (*A. hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. *Global Change Biology*, **9**:1775-1787.
29. THOMPSON LK, M ZIV AND GF DEITZER (1985). Photo control of peanut (*A. hypogaea* L) embryo and ovule development in vitro. *Plant Physiology*, **78**: 370-373.
30. THOMPSON LK, BURGESS CL AND SKINNER EN (1992). Localization of phytochrome during peanut (*A. hypogaea*) gynophore and ovule development. *American Journal of Botany*, **79**:828-832.
31. ZHU WEI, X CHEN, H LI, F ZHU, Y HONG, RK VARSHNEY AND X LIANG (2014). Comparative transcriptome analysis of aerial and subterranean pods development provides insights into seed abortion in peanut. *Plant Molecular Biology*, **85**: 395-409.
32. SMITH BW (1954). *A. hypogaea* Reproductive efficiency. *American Journal of Botany*, **41**:607-616.
33. ZHARARE GE, FPC BLAMEY AND CJ ASHER (1998). Initiation and morphogenesis of groundnut (*A. hypogaea* L.) pods in solution culture. *Annals of Botany*, **81**:391-396.
34. COX FR, GA SULLIVAN AND CK MARTIN (1976). Effect of calcium and irrigation treatments on peanut yield, grade and seed quality. *Peanut Science*, **3**:81-85.
35. BELL MJ, GC WRIGHT AND GL HAMMER (1992). Night temperature affects radiation use efficiency in peanut. *Crop Science*, **32**: 1329-1335.
36. BELL MJ, DJ BAGNALL AND G HARCH (1991). The effects of photoperiod on reproductive development of Peanut (*A. hypogaea* L.) in a cool subtropical environment 2. temperature interactions. *Australian Journal Agricultural Research*, **42**: 1151-1161.
37. WILLIAMS JH, JHH WILSON AND GC BATE (1975). The growth of groundnuts (*A. hypogaea*) at three altitudes in Rhodesia. *Rhodesian Journal Agricultural Research*, **13**:33-43.
38. NIGAM SN, RCN RAO, JC WYNNE, JH WILLIAMS, M FITZNER AND GVS NAGABHUSHANAM (1994). Effect and interaction of temperature and photoperiod on growth and partitioning in three groundnut (*A. hypogaea* L.) genotypes. *Annals of Applied Biology*, **125**: 541-552.
39. GOLOMBEK SD AND JOHANSON (1997). Effect of soil temperature on vegetative and reproductive growth and development in three Spanish genotypes of peanut (*A. hypogaea*). *Peanut Science*, **24**: 67-72.
40. VARA PRASAD PV, PQ CRAUFURD AND RJ SUMMERFIELD (2000). Effect of high air and oil temperature on dry matter production, pod yield and yield components of groundnut. *Plant Soil*, **222**: 231-239.
41. OMIMA BHH, HAA AHMED, MF ADEL AND ASA AMIN (2018). Variability Heritability and Genetic Advance of Some Groundnut Genotypes (*A. hypogaea* L.) under Saline Sodic Soil. *Annual Review of Materials Research*, **1**(1): 554-555.
42. NAKASHIMA K AND K YAMAGUCHI-SHINOZAKI (2013). ABA signalling in stress-response and seed development. *Plant Cell Reports*, **32**: 959-970.
43. THANEENART S AND S NUAN-ON (1987). Seed quality of peanut (*A. hypogaea* L.) from harvest at different stages. *Seed Science and Technology*, **15**:613-616.
44. SINGH AL, PC NAUTIYAL AND V ZALAP (1998). Growth and yield of groundnut varieties as influenced by seed size. *Tropical Science*, **38**:48-56.
45. DEVI DAYAL, PK GHOSH AND V RAVINDRA (1999). The influence of seed maturity variation on crop establishment, growth, and yield of groundnut (*A. hypogaea* L.). *Tropical Agriculture (Trinidad)*, **76** (3):151-156.
46. FINCH-SAVAGE WE AND GW BASSEL (2015). Seed vigour and crop establishment: extending performance beyond adaptation. *Journalof Experimental Botany*, **67**(3): 567-591.
47. LEPRINCE OLIVER, A PELLIZZARO, S BERRIRI AND J BUITINK (2017). Late seed maturation: drying without drying. *Journal of Experimental Botany*, **168**(4):827-841.
48. GILMAN DF AND SMITH (1977). Internal pericarp colour as a subjective maturity index for peanut breeding. *Peanut Science*, **4**: 67-70.

49. SANDERS TH (1989).Maturity distribution in commercially sized Florunner peanuts. *Peanut Science*,**16**: 91-95.

50. RUCKER KS, CK KVIEN, K CALHOUN, RJ HENNING, PE KOEHLER, SR GHATE AND CC HOLBROOK (1994). Sorting peanut by pod density to improve quality, kernel maturity distribution, and reduce aflatoxin. *Peanut Science*, **21**:147-152.

51. YOUNG CT AND ME MASON (1972). Free arginine content of peanut (*A. hypogaea*) as a measure of seed maturity. *Journal of Food Science*, **37**:722-725.

52. NIGAM SN (2014). Groundnut at a glance. pp: 121.

53. MISRA JB (2004). A mathematical approach to comprehensive evaluation of quality in groundnut. *Journal of Food Composition and Analysis*, **17**: 69-79.

54. ADAMS JF, DL HARTZANG AND DB NELSON (1993). Supplemental calcium application on yield, grade, and seed quality of runner peanut. *Agronomy journal*, **85**: 86-93.

55. NAUTIYAL PC, JB MISRA AND PV ZALA (2010). Influence of seed maturity stages on germinability and seedling vigour in groundnut. *Journal of SAT Agricultural Research*, **8**:1-8.

56. NAUTIYAL PC (2009). Seed and seedling vigour traits in groundnut (*A. hypogaea* L.). *Seed Science and Technology*, **37**: 721-735.

57. WANEENART S AND S NUAN-ON (1987). Seed quality of peanut (*A. hypogaea* L.) from harvest in different stages. *Seed Science and Technology*, **15**: 613-616.

58. NAUTIYAL PC, AL RATHNAKUMAR, PARESH SODAVADIYA, PV ZALA, HB LALWANI AND LATARAWAL (2019). Diversity of root and shoot traits associated with drought tolerance in groundnut germplasm and advanced breeding materials. *The Journal of Food, Agriculture and Environment*, **17**(1): 18-29.

59. NAUTIYAL PC, YC JOSHI AND PV ZALA (1991). A storage method to prolong seed viability in groundnut. *International Arachis Newsletter*, **9**:21-22.

60. MUSINGO MN, SM BASHA, TH SANDERS, RJ COLE AND BLANKENSHIP (1989). Effect of drought and temperature stress on peanut (*A. hypogaea* L.) seed composition. *Journal of Plant Physiology*, **134**: 710-715.

61. KETRING DL (1992). Physiology of oil seeds. X. Seed quality of peanut genotypes as affected by ambient storage temperature. *Peanut Science*, **19**(2):72-77.

62. BUITINK J AND O LEPRINCE (2004). Glass formation in plant anhydrobiotes: survival in the dry state. *Cryobiology*, **48**: 215–228.

63. MADHUSUDHAN RAO, DVV NARAYANA AND PG REDDY (1975). The effect of sun and shade drying and different methods of storage on the viability of bunch groundnut (*A. hypogaea* L.). *Oilseeds Journal*, **4**:39-41.

64. NAUTIYAL PC, V RAVINDRA AND PV ZALA (2001a). A new method for drying groundnut pods for better seed storability. *International Arachis Newsletter*, **21**:26-30.

65. NAUTIYAL PC AND PV ZALA (1991). Effect of drying methods on seed viability and seedling vigour in Spanish groundnut (*A. hypogaea* L.). *Seed Science and Technology*, **19**:451-459.

66. NAUTIYAL PC, A BANDYOPADHYAY AND RC MISRA (2004). Drying and storage method to prolong seed viability of summer groundnut (*A. hypogaea* L.) in Orissa. *Indian Journal of Agricultural Sciences*, **74**: 316-320.

67. FERNANDEZ EM, CA ROSOLEM AND DM OLIVEIRA (2000). Peanut seed tegument is affected by liming and drying method. *Seed Science and Technology*, **27**: 185-192.

68. NAUTIYAL PC AND JB MISRA (2005). Effect of drying methods on seed germination and seed-protein profile in groundnut. *Journal of Oilseeds Research*, **22**:125-128.

69. NAUTIYAL PC AND GANESH KULKARNI (2009). Seed SDS-PAGE protein profile in dormant and non-dormant types of groundnut (*A. hypogaea*) cultivars. *Indian Journal of Agricultural Sciences*, **79**:476-478.

70. BUITINK J, FA HOEKSTRA AND O LEPRINCE (2002). Biochemistry and biophysics of tolerance systems. In: Black M and Pritchard H W (Editors). Desiccation and survival in plants: drying without dying. CABI Publishing, Wallingford, Oxford, pp: 293-318.

71. BERJEK P, JM FARRANT AND NW PAMMENTER (2007). Seed desiccation tolerance In Plant Desiccation Tolerance (eds) Jenks MA, and Wood AJ, Black Well Publishing, pp:151-192.

72. SUBBARAMAN R AND JACQUELINE AS (1989). Effect of method of shelling and pod moisture on viability of groundnut seed in storage. Seed and Farms, pp:11-16.

73. GHEWANDE MP, G NAGRAJ, S DESAI AND P NARAYAN (1993). Screening of groundnut bold-seeded genotypes for resistance to *Aspergillus flavus* seed colonisation and less aflatoxin production. *Seed Science and Technology*, **21**: 45-51.

74. CEMAL KURT, ERDEM, TUNAHAN, BAKALHALIL, EL ARIOGLUHALIS AND SABAGH AYMAN (2016). Peg strength of eight peanut cultivars grown in Mediterranean conditions. Retrieved from 10.14196/sjcs.v5i7.2253. *Scientific Journal of Crop Science*, **5**:121-124.

75. SUN WQ (1997). Glassy state and seed storage stability: the WLF kinetics of seed viability loss at T>Tg and the plasticization effect of water on storage stability. *Annals of Botany*, **79**:291-297.

76. SATTLER SE, LU GILLILAND, M MAGALLANES-LUNDBACK, M POLLARD AND D DELLAP (2004). Vitamin E is essential for seed longevity and for preventing lipid peroxidation during germination. *Plant Cell*, **16**:1419–1432.

77. NAVARRO S, E DONAHAYE, R DIAS AND E JAY (1989). Integration of modified atmospheres for disinfestations of modified atmospheres for disinfestation of dried fruit. Final Scientific report of Project No:I-1095-1086 submitted to US-Israel BI-National Agricultural Research and Development Fund (BARD). pp: 86.

78. HONG-YAN C, Z GUANG-HUA, J XIN-MING, *ET AL.* (1997). Storage of peanut seeds with low moisture content for 11 years in ambient temperature. *Plant genetic Resources Newsletter*, **110**: 35-40.

79. NAUTIYAL PC AND V RAVINDRA (1996). Drying and storage method to prolong seed viability and seedling vigour of rabi-summer-produced groundnut. *Journal of Agronomy and Crop Science*, **177**: 123-128.

80. BARBOSA RM, JULIANA FARIA DOS SANTOS, MAGNOLIA DE MENDONCA LOPES, RITA DE CASSIA PANIZZI AND ROBERVAL DAITON VIEIRA (2013). Chemical control of pathogens and the physiological performance of peanut seeds. *Journal of Food, Agriculture and Environment*, **11**(2): 322-326.

81. NAUTIYAL PC, RAVINDRAV AND YC JOSHI (1989a). Varietal and seasonal variation in seed viability among Spanish

groundnut (*A. hypogaea* L.). *Indian Journal of Agriculture Science*, **60**: 143-145.

82. KETRING DL (1973). Ethylene production, germination, and vigour of Starr variety Spanish type peanut seeds stored at high and low humidity. *Proceedings American Peanut Research and Education*, **5**: 114-122.
83. ANONYMOUS (2008). Directorate of Groundnut Research Annual Report, Junagadh.
84. NAUTIYAL PC AND YC JOSHI (1991). Storage of rabi/summer groundnut (*A. hypogaea* L) with calcium chloride for prolonged seed viability and vigour. Tropical Science, **31**: 21-26.
85. NAUTIYAL PC, YC JOSHI AND PV ZALA (1996).A storage method to prolong seed viability in groundnut (*A. hypogaea* L.). *Agri-Equipment International*, **48**: 3-4.
86. NAUTIYAL PC, YC JOSHI AND DEVI DAYAL (2002). Response of groundnut to deficit irrigation during vegetative growth. FAO. *Water Report*, **22**: 39-46.
87. WALTERS C (1998). Understanding the mechanisms and kinetics of seed ageing. *Seed Science Research*, **8**(2): 223-244.
88. WILSON DO (JR) AND MB MCDONALD (JR) 1986.The lipid peroxidation model of seed ageing. *Seed Science and Technology*, **14**(2): 269-300.
89. MCDONALD MB (2004). Orthodox Seed Deterioration and Its Repair. In: Benech-Arnold, R.L. and Sánchez, R.A., Eds., Handbook of Seed Physiology, Application to Agriculture, Haworth Press, Inc., New York, pp: 273-298.
90. MORTON BR (2007). Poor field performance of late maturing peanut cultivars (*A. hypogaea* L.) derived from PI-I03396. A dissertation presented to the Graduate School of the University of Florida in partial fulfilment of the requirements for the degree of Doctor of Philosophy, University of Florida.
91. LEYLA GULLUOGLU, HALILBAKAL, BIHTERONAT, CEMAL KURT AND HALISARIOGLU (2016). The effect of harvesting on some agronomic and quality characteristics of peanut grown in the Mediterranean region of Turkey. Retrieved from http// doi: 10.17557/tife.20186. *Turkish Journal of Field Crops*, **21**(2): 224-232.
92. BAILLY C (2004). Active oxygen species and antioxidants in seed biology. *Seed Science Research*, **14**: 93–107.
93. BUCKERIDGE MS (2010). Seed cell wall storage polysaccharide: Model to understand cell wall biosynthesis and degradation. *Plant Physiology*, **154**:1017-1023.
94. CANAVAR Ö (2014). The influence of storage time on fatty acid, tocopherol and seed quality of peanut. Retrieved from https:// doi.org/10.3920/QAS2013.0276. *Quality Assurance and Safety of Crops & Foods*, **7**(2):165–174.
95. SUNG JM AND JENG TL (1994). Peroxidation and peroxide-scavenging enzymes associated with accelerated ageing of peanut seed. *Physiology Plant*, **91**(1): 51-55.
96. MORAD S, RA ABASALT, DM GHORBAN AND TAHMINE (2013). Review on dual role of reactive oxygen species in seed physiology and germination. *International Journal of Agricultural Crop Science*, **5**(20): 2390-2393.
97. NEERGAARD P (1977). Seed pathology, The Macmillan Press Ltd, London UK, **3**: 519-839.
98. MORTON BR, BL TILLMAN, DW GORBET AND KJ BOOTE (2008). Impact of seed storage environment on field emergence of peanut (*A. hypogaea*) cultivars. *Peanut Science*, **35**(2): 108-115.
99. SILVA AT, AR PAMELA, LC RAQUEL, L WILCO AND WMH HENK (2016). A predictive co expression network identifies novel gene controlling the seed-to-seed seedling phase transition in *Arabidopsis thaliana*. *Plant Physiology*, **170**: 2218-2231.
100. BEWLEY JD AND M BLACK 1994. Seed physiology of development and germination. 2nd edition. Plenum Press, New York.
101. ISTA (2019). International Rules for Seed Testing, Full Issue i–19-8 (300). The International Seed Testing Association (ISTA), Zürichstr. 50, CH-8303 Bassersdorf, Switzerland.
102. SAMAD IMA AND RS PEARCE (1978). Leaching of ions, organic molecules and enzymes from seeds of peanut imbibing without intact testa. *Experimental Botany*, **29**(6):1471-1478.
103. NAUTIYAL PC, YC JOSHI AND PV ZALA (1994). Screening of Spanish groundnut cultivars for germination under simulated drought stress. *International Arachis Newsletter*, **14**: 22.
104. NAUTIYAL PC, VRAVINDRA AND JBMISRA (1997). Response of dormant and non-dormant seeds of groundnut (*A. hypogaea*) genotypes to accelerated ageing. *Indian Journal of Agricultural Science*, **67** (2): 67-70.
105. NAUTIYAL PC AND PV ZALA (2004). Influence of drying methods and temperatures on germinability and vigour of groundnut (*A. hypogaea* L.) seed harvested in summer season. *Indian Journal of Agricultural Science*, **74**: 588-93.
106. SIDDIQUE MA AND PB GOODWIN (1985). Conductivity measurements on single seeds to predict the germinability of French beans. *Seed Science and Technology*, **13**: 643–652.
107. MORGAN PW, DL KETERING, EM BEYER (JR) AND JA LIPE (1970). Function of naturally produced ethylene in abscission, dehiscence, and seed germination. P. 502-509. In Carr D. J. (ed) Plant growth substances. Proc. 7th International Symposium: Plant Growth Substances Canberra, Australia. 7th Dec 1970. Springer-Verlag, Berlin, Heidelberg-New York.
108. BITTENCOURT SR AND RD VIEIRA (1996). Use of reduced concentration of tetrazolium for evaluation of the viability of peanut seed lots. *Seed Science and Technology*, **25**:75-82.
109. MOHAMED HA, JA CLARK, AND CK ONG (1988). Genotypic differences in the temperature responses of tropical crops I. Germination characteristics of groundnut (Arachis hypogaea L.) and pearl millet (*Pennisetum typhoides* S & H). *Journal of Experimental Botany*, **39**:1121– 1128.
110. MISRA JB, PC NAUTIYAL AND SHEELA CHAUHAN (1994). Catabolism of oil and protein and biosynthesis of starch in the cotyledons of germinating seeds of groundnut*. Plant Physiology Biochemical*, **21**:18-21.
111. HARRISON KD, IBRAHIM MOHAMMED AND TA RICHARDD (2014). Phenological development and yield of three groundnut varieties as influenced by plant density in a forest-savanna transition zone. *International Journal of Agricultural Research*, **9**: 87-98.
112. SINGH RUKAM, DEEPAK ISSAR, PV ZALA AND PC NAUTIYAL (2007). Variation in sensitivity to salinity in groundnut cultivars during seed germination and early seedling growth. *Journal SAT Agricultural Research*, **5**:1-7.
113. KETRING DL (1991). Physiology of oil seeds: IX Effects of water deficit on peanut seed quality. *Crop Science*, **31**:459-463.

114. NAUTIYAL PC, A BANDYOPADHYAY AND PV ZALA (2001b). In situ sprouting and regulation of fresh seed dormancy in Spanish type groundnut (*A. hypogaea* L). *Field Crop Research*, **70**: 233-241.

115. BANDHYOPADHYAY A, PC NAUTIYAL, T RADHAKRISHAN AND HK GOR (1999). Role of testa, cotyledon and embryonic axis in seed dormancy of groundnut (*A. hypogaea* L.). *Journal of Agronomy Crop Science*, **182**: 37-41.

116. NAUTIYAL PC, A BANDYOPADHYAY AND V RAVINDRA (1999b). Nature of fresh-seed dormancy in peanut. *Food legume Newsletter (ACIAR) Australia*. **30**: 5-6.

117. UPADHYAYA HD AND SN NIGAM (1999). Inheritance of fresh seed dormancy in peanut. *Crop Science*, **39**: 98-101.

118. YAW AJ, A RICHARD, OSEI SAFO-KANTANKA, HK ADU-DAPAAH, S OHEMENG-DAPAAH, AND A ADELAIDE (2008). Inheritance of fresh seed dormancy in groundnut. *African Journal of Biotechnology*, **7**:421-424.

119. KHALFAOUI JLV (1991). Inheritance of seed dormancy in a cross between two Spanish peanut cultivars. *Peanut Science*, **18**: 65-67.

120. NAUTIYAL PC, A BANDYOPADHYAY AND V RAVINDRA (1993). Problems with defining seed dormancy characteristics of groundnut genotypes. *Journal of Oilseeds Research*, **10**(2):271-276.

121. BASBOUSS-SERHAL ISABELLE, L SOUBIGOU-TACONNAT, C BAILLEY AND J LEYMARIE (2015). Germination potential of dormant and non-dormant *Arabidopsis* seeds is driven by distinct recruitment of messenger RNAs to polysomes. *Plant Physiology*, **168**:1049-1065.

122. SANDERS TH, JA LANSDEN, RL GREENE, JS DREXLER AND EJ WILLIAMS (1982). Oil characteristics of peanut fruit separated by non-destructive maturity classification method. *Peanut Science*, **9**:20-23.

123. ZADE VR, SN DESMUKH AND PS REDDY (1986). Magnitude of dormancy in the released Virginia group cultivars of peanut. *Seed Research*, **14**: 235-238.

124. TOOLE VK, WK BAILEY AND EH TOOLE (1964). Factors influencing dormancy of peanut seeds. *Plant Physiology*, **39**:822-832.

125. ARJUNAN A AND PS SRINIVASAN (1989). Pre-sowing seed hardening for drought tolerance in groundnut. *Madras Agricultural Journal*, **76** (9): 523-528.

126. DHEDHI KK, CJ DANGARIA, GJ PARSANA AND AK JOSHI (2007). Effect of pre-sowing seed treatments for better crop establishment in summer groundnut, *Seed Research*, **35**(1): 12-21.

127. FU XH AND JR FU (1990). The effect of osmoconditioning with PEG on the increase in vigour and cold hardness of groundnut seeds. *Acta Scintia Nation Universitates Sunyatsene*, **29**(1):63-70.

128. FU JR, SH LUS, RZ CHEN, BZ ZHANG, ZS LIU AND DY CAI (1988). Osmoconditioning of peanut seed with PEG to improve vigour and some biochemical activities. *Seed Science and Technology*, **16**:197-212.

129. JOSHI YC, PC NAUTIYAL AND V RAVINDRA (1996). Screening for cold tolerance and osmoconditioning to enhance germination of groundnut in suboptimal temperatures. *Tropical Science*, **36**: 224-228.

130. NAUTIYAL PC, VRAVINDRA AND YCJOSHI (1989b). Germination and early seedling growth of some groundnut (*A. hypogaea* L.) cultivars under salt stress. *Indian Journal of Plant Physiology*, **32**: 251-253.

131. BABUVANKATESH D, SBALAJI NAYAK AND PSUJATHAMMA (2018). Studies on seed priming on seedling vigour, crop growth and yield of groundnut under rain-fed condition. *International Journal of Pure & Applied Bioscience*, **6** (5): 238-242.

132. KRISHNA SK AND YNATARAJAN (2016). Effect of nanoparticles in volatile production during seed storage of groundnut. *International Journal of Agriculture Sciences*, **12**(2):191-198.

133. BHAUSO TD, TRADHAKRISHNAN, AKUMAR, GPMISRA, JRDOBARIA, *ET AL.* (2014). Over expression of bacterial mtlD gene confers enhanced tolerance to salt stress and water deficit stress in transgenic peanut through accumulation of mannitol. Australian *Journal of Crop Science*, **8**:413-421.

134. GANGURDE SS, RAKESH KUMAR, AK PANDEY, MARK BAROW, EL HAYDEE, SPURTHI N NAYAR, BAOZHU GUO, BOSHOU LIAO, RAMESH S BHAT, NAGA MADHURI, S HEMALATHA, HARI K SUDINI, PASUPULETI JANILA, PUTTA LATHA, HASAN KHAN, BABU N MOTAGI, T RADHAKRISHNAN, NAVEEN PUPPALA, RAJEEV K VARSHNEY AND MANISH K. PANDEY 2019. Climate smart groundnuts for achieving high productivity and improved quality: Current status, challenges and opportunities. In: Kole C (ed) Genomic designing of climate smart oilseed crops, Springer, Cham. Retrieved from http.//doi.org/10.1007/978-3-319-93536-2-3, Pp:133-172.

135. PANDEY MK, E MONYO, P OZIAS-AKINS, X LIANG, P GUIMARÃES, N NIGAMS, *ET AL.* (2012).Advances in *Arachis* genomics for peanut improvement. Retrieved from doi: 10.1016/j.biotechadv.2011.11.001, *Biotechnology Advances*, **30**, 639–651.

136. CHU Y, CC HOLBROOK AND P OZAIS-AKIN (2009). Two alleles of ahFAP2B control the high oleic acid trait in cultivated peanut. *Crop Science*, **49**: 2029-2036.

137. CHEN X, H LI, MK PANDEY, Q YANG AND X WANG (2016). Draft genome of the peanut A- genome progenitor (*A. duranensis*) provide insight into geocarpy, oil biosynthesis and allergens. *Proceedings of the National Academy of Sciences of the United States of America*, **113** (24): 6785-6790.

138. JANILA P, MK PANDEY, Y SHASIDHAR, MT VARIATH, M SRISWATHI *ET AL.* (2016). Molecular breeding for introgression of fatty acid desturase mutant alleles (ahFAD2A and ahFAD2B) enhances oil quality in high and low oil containing peanut genotypes. *Plant Science*, **242**: 203-213.

139. SARVAMANGALA C, MV GOWDA AND RK VARSHNEY (2011). Identification of quantitative traits for protein content, oil content, and oil quality for groundnut, *Field Crop Research*, **122**: 49-59.

140. SHASIDHAR Y, MK VISHWAKARMA, MK PANDEY, P JANILA AND MT VARIATH *ET AL.* (2017). Molecular mapping of oil content and fatty acid using dense genetic maps in groundnut. *Front Plant Science*, **8**: 794.

141. HAYAT-EL-MAAROUF-BOUTEAU (2013). Role of protein and m-RNA oxidation in seed dormancy and germination, Retrieved from http// doi:10.3389/fpls.2013.00077.

142. FINCH-SAVAGE WE AND MG LEUBNER (2006). Seed dormancy and control of germination. *New Phytologist*, **171**: 501-523.

143. VISHWAKARMA MK, MK PANDEY, Y SHASHIDHAR, SS MANOHAR AND P NAGESH, *ET AL.* (2016). Identification of two major quantitative trait locus for fresh seed dormancy using diversity arrays technology and diversity arrays technology-seq based genetic map in Spanish type peanuts. *Plant Breeding*, **135**(3): 367-375.

144. ZHANG X, J ZHANG, X HE, Y WANG AND X MA, *ET AL*. (2017). Genome-wide association study of major agronomic traits related to domestication in peanut. *Frontiers in Plant Science*, **26**(8): 1611.

145. PRIETO-DAPENA PP, R CASTANO, C ALMOGUERA AND J JORDANO (2006).Improved resistance to controlled deterioration in transgenic seeds. *Plant Physiology*, **142**(3): 1102-1112.

146. NAUTIYAL PC AND SHONO M (2010). Analysis of the role of mitochondrial and endoplasmic reticulum localized small heat-shock proteins in tomato (*Lycopersicon esculentum* Mill.) plant. *Biologia Plantarum*, **54** (4):715-719.

147. PYTON P, KR KOTTAPALI, D ROWLAND AND W FAIRCLOTH ET AL., (2009). Gene expressing profiling in peanut using high density oligonucleotide microarrays. Retrieved from doi 10.1186/147-2164-10-265, *BMC Genomics*, **10**:265.

148. SOTI C AND YP CSERMEL (2007). Protein stress and stress proteins: implication in ageing and diseases. *Journal of Biosciences*, **32**: 511-515.

149. RAJJOU L, Y LOVIGNY, SPC GROOT, M BELGHAZI AND C JOB, *ET AL.* (2008). Proteome-wide characterization of seed ageing in *Arabidopsis*: a comparison between artificial and natural ageing protocols. *Plant Physiology*, **148**:620-641.

150. SUNKARA S, PBHATNAGAR-MATHUR AND KKSHARMA (2014). Isolation and functional characterization of a novel seed-specific promoter region from peanut. *Applied Biochemistry and Biotechnology*,**172**:325-339.

151. YAN HAIYAN, JIAQUAN HUANG, BOSHOU LIAO, XIANQING LAN, QIUTING LUO, JUNLONG TANG (2012). DOF transcription factors in developing peanut (*A. hypogaea*) seeds. *American Journal of Biochemistry and Molecular Biology*, **9**, 2:60-71.

152. NAWADE B, CBTAJES, TRADHAKRISHNAN, LRARULTHAMBI, ABHAY KUMAR, JRDOBARIA, RAHUL KUNDU AND GPMISHRA (2016). Insights into the Indian Peanut Genotypes for ahFAD2 Gene Polymorphism Regulating Its Oleic and Linoleic Acid Fluxes, Retrieved from https://www.frontiersin.org/article/10.3389/fpls.2016.01271,doi:10.3389/fpls.2016.01271, *Frontiers in Plant Science*, **7**:1271.

153. SMITH BW (1950). Arachis hypogaea. Aerial Flower and Subterranean Fruit. *American Journal of Botany*, **37**(10): 802-815.

154. WANG X, PXU, LYIN, YREN AND SLI, *et al.* (2018). Genomic and transcriptomic analysis identified gene clusters and candidate genes for oil content in peanut*. Plant Molecular Biology Report*, **36:518.**